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**A NEW DIPTEROCARP-ASSOCIATED GALL-INHABITING COCCOID FROM
BORNEO (HOMOPTERA: COCCOIDEA)**

By SADAO TAKAGI and CHRIS J. HODGSON

Abstract

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Danumococcus parashoreae, gen. et sp. nov., is described on the basis of specimens collected at Danum Valley, Sabah, Malaysia, on the leaves of *Parashorea tomentella* (Dipterocarpaceae). The adult female inhabits a small lenticular gall induced on the blade. The gall has a small round opening at the centre of the roof. The male normally occurs outside the gall, and secretes a loose mass of wax to form a cocoon around the body in the second instar. The adult female is extremely degenerate, having no setiferous antennae, no legs, and no disc pores. It has been unusually modified in several other features and is provided with some peculiar, remarkably developed structures, apparently associated with the opening in the roof of the lenticular gall. The first-instar female and the first- and second-instar and adult males, the stages probably not or less modified in association with the gall structure, have some features similar to those in *Beesonia*, *Mangalorea*, *Gallacoccus*, and *Echinogalla*. The view is adopted tentatively that the gall-inhabiting coccoids of these genera and *Danumococcus*, though far from uniform, belong to the same phylogenetic group, the family Beesoniidae, which has evolved mainly on dipterocarps. However, the second-instar male of *Danumococcus* is provided with clusters of deeply concave disc pores similar to those on *Dactylopius*. This fact may suggest the presence of some phylogenetic relationship between *Danumococcus* and *Dactylopius* and, further, may promote the concept of a broader natural group comprising all the genera mentioned above and others now in separate families. A cladistic analysis based on macropterous male characters shows that *D. parashoreae* belongs to the Beesoniidae and also that the Beesoniidae and the Stictococcidae fall within a larger clade which includes the Dactylopiidae and some gall-inducing eriococcids.

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Contents. Introduction — Description (*Danumococcus*, gen. nov.; *Danumococcus parashoreae*, sp. nov.) — Features and a taxonomic view (Features and their functions; A taxonomic view) [by TAKAGI] — Taxonomic position based on the morphology of the adult male (Introduction; Materials and methods; Results; Discussion; Conclusions) [by HODGSON] — Coccoid genera and species mentioned in the text and Fig. 21 — Acknowledgements — References — Figures.

INTRODUCTION

Up to the present, eight species of dipterocarp-associated gall-inhabiting coccoids (DGC's) have been formally described from tropical Asia in four genera: two species in *Beesonia* (which also includes two other species associated with oaks in warm-temperate eastern Asia), one species in *Mangalorea*, four species in *Gallacoccus*, and one species in *Echinogalla*. These genera are diverse in their character patterns, and the classification of them at the family level has not been definitely settled. Recently, the former two genera have been referred to the Beesoniidae and the latter two to the Eriococcidae, but this separation of the genera into the different families is not without question (Takagi, 2001). Hodgson (2001) included representatives of all of the above genera in a cladistic analysis based on the morphology of macropterous adult males. In his study, these genera came out very clearly in a single clade.

Anthony (1980) and Jenkins (1992) examined herbarium specimens of dipterocarps for galls similar to those induced by *Gallacoccus anthonyae*, *G. secundus*, and *Mangalorea hopeae*, and found such galls on many species of dipterocarps. Thus, their examinations suggest the occurrence of an unknown number of DGC's over the distribution range of the Dipterocarpaceae in Asia and Africa. The galls induced on dipterocarps actually or presumably by coccoids are diverse in external appearance, representing some distinct types. The gall induced by *Beesonia dipterocarpi* is a conglomeration of hypertrophied leaf-buds and contains many adult females (Green, 1928), whereas *Beesonia shoreae* induces a small, simple pit gall on the twig inhabited by a single female or male. *Gallacoccus anthonyae* induces an elongate gall composed of overlapping scales, and many dipterocarps of the genus *Shorea* bear galls of this type. Other galls occurring on various dipterocarps are globular and equipped with eminent, spinous external appendages, thus being breadfruit- or durian-like in appearance, as exemplified by the galls induced by *Mangalorea hopeae*, *Gallacoccus spinigalla*, and *Echinogalla pustulata*. Galls adorned with hairy, folious, fibrous, or wiry appendages are also formed on dipterocarps. Globular, pear-shaped, or compressed galls without external appendages are known mainly on *Shorea* species, and the galls induced by *Gallacoccus secundus* and *G. heckrothi* represent this type. The mentioned coccoids show that galls induced by coccoid species of the same genus do not necessarily belong to the same type, and that galls of the same type may be induced by coccoids belonging to different genera. Galls of various types are also induced by coccoids belonging to the single genus *Apiomorpha* (Gullan, 1984).

The coccoid described in this paper, representing a new genus and a new species, induces another distinct type of gall. It was collected at Danum Valley, Sabah, on *Parashorea tomentella*, so that it is named *Danumococcus parashoreae*. This species is so unique and peculiar in the external features of the adult female that it is not easy to find its relationship to other known coccoids. The adult male is beset with "papillae" on the body as in *Mangalorea*, *Gallacoccus*, and *Echinogalla*. The first-instar female and male do not much differ from those of *Echinogalla pustulata*. The significance of these facts is still not clear, but the possibility that *Danumococcus* is related to other DGC's phylogenetically should not be rejected. On the other hand, the second-instar male of *D. parashoreae* possesses clusters of deeply concave quinquelocular disc pores, whereas *Dactylopius* has similar disc pores. According to recent authors (Perez Guerra and Kosztarab, 1992, and others), *Dactylopius* alone constitutes the family Dactylopiidae,

comprising nine species exclusively associated with cacti and, therefore, originally restricted to America in distribution. Furthermore, none of the species are gallicolous.

The discovery of the new form, thus, does not help to settle the taxonomic question on DGC's but has made it more perplexing. Furthermore, it suggests that there are other unpredictable forms of DGC's to be discovered.

In a cladistic study based on characters of adult females and nymphs, Foldi (1995) united the tropical South American genus *Limacoccus* with *Beesonia* and *Mangalorea* in the same family. This affiliation has made the matter more complicated, because *Limacoccus*, represented by four known species, is exclusively associated with palms and, according to Foldi, related also to the palm-associated families Phoenicococcidae and Halimococcidae. In addition, no gall-inducing species are known in all these palm-associated taxa. In the present study, *Limacoccus* is excluded from consideration. The problem may better be postponed for a discussion including the adult male of *Limacoccus*.

DESCRIPTION

Danumococcus Takagi and Hodgson, gen. nov.

Type species. *Danumococcus parashoreae*, sp. nov.

First-instar female and male. Beset with a number of small swellings over the dorsal surface and marginally on the ventral surface, especially remarkably in the female. Antennae 3-segmented, the second segment very short and the third twice as long as wide. Dorsal setae blunt or clavate apically except some ones in the male. Small ducts occurring submedially on the dorsal surface and also along the body margin mostly on the ventral surface. Anus indiscernible.

Adult female. Inhabiting a leaf gall. Peculiar in having an eminent sclerotized tubercle (called "hump" in the description below), which is situated in front of the anus, entirely covered with a thin operculum, and accompanied with strong scleroses anteriorly. Vulva longitudinal on the midline of the body. A pair of large, membranous, discoid structures present between the anus and vulva and nearer to the vulva. Dense setae forming a continuous series around the posterior half of the hump to around the vulva. Other features are degenerative, and there are no setiferous antennae, no legs, and no disc pores. Minute ducts present.

Second-instar male. Provided with clusters of deeply concave 5-locular disc pores on the dorsal surface in addition to 5-locular disc pores of the usual type occurring singly on the ventral surface. Ducts present on both surfaces. Antennae 3-segmented, the second segment very short and the third twice as long as wide.

Adult male. Macropterous, with well-developed sclerites on the head and thorax. Antennae 7-segmented, the apical segment with stiff, apically knobbed setae. "Papillae" or fleshy nipple-like processes of the derm occurring on the head, antennae, legs, and trunk. Abdomen without glandular pouches and accompanying long setae on the eighth segment. Genital segment elongated into a slender style (penis sheath).

Danumococcus parashoreae Takagi and Hodgson, sp. nov.

Material. Collected in the Danum Valley Conservation Area, Ulu Segama, Bahagian Tawau, Sabah [on the island of Borneo], Malaysia, on the leaves of *Parashorea tomentella* (Dipterocarpaceae), 24 October 1988 [material no. 88ML-195].

Adult females were obtained from within galls induced on the blade between veins. A fully formed gall (Figs 1, 7, 8), inhabited by a single adult female (and sometimes also by a few male nymphs: see below), is small and inconspicuous, nearly round in outline, at most about 1.5mm across, and lenticular in shape, being gently swollen on both upper and lower surfaces of the leaf. In cross section, the gall-forming portions of the upper and lower layers of the leaf are hardened on the surface and curved to form a transverse subrhombic space between them, which is nearly fully occupied by the body of the adult female. The gall has a small round opening, a little more than 0.1mm across, at the centre on one side, which is on the upper or lower surface of the leaf and represents the roof (and the ceiling in the interior) of the gall, the female feeding on the inner wall of the opposite side (or the floor). In dry material, the gall is brown and glossy, with a narrow pale brown ring around the opening.

Female crawlers were collected on both upper and lower surfaces of the leaf outside the gall. Male nymphs of the first and second instars were found on the lower surface of the leaf around galls, the second-instar males secreting wax around the body. Male nymphs were also obtained from within galls, in which, however, all the second-instar males found were naked, secreting no wax. The adult males collected were each found within a test or cocoon (Figs 1, 9) formed on the lower surface of the leaf outside the gall; they were teneral, and most of the slide-mounted specimens are badly distorted.

Holotype. First-instar female, deposited in the collection of the Forest Research Institute of Malaysia, Kepong, Kuala Lumpur.

First-instar female (Fig. 2). The examined specimens, apparently at the crawling stage, are nearly obovate; segmentation obscure; thorax occupying a greater part of the body; abdomen small, the sterna of some posterior segments being condensed and fused together. Dorsal surface densely beset with a number of small sclerotized swellings, which are somewhat variable in size but mostly round in outline; ventral surface also with such swellings marginally, and with transverse rows of spicules medially between the mid coxae and on several basal segments of the abdomen. Dorsal setae stout, blunt or clavate apically, occurring along the body margin and also in the submedian and intermediate regions, variable in size, most of the setae occurring along the body margin longer than the others; on the ventral surface, several blunt or clavate setae occurring along the head margin; ventral setae of the abdomen crowded towards the apex of the body owing to the condensed sterna, comprising a pair of blunt setae occurring submedially near the apex of the abdomen and a group of some short, spinous setae in front of the blunt setae. Long caudal setae absent. Minute ducts present, occurring as follows on each side: 5 submedians on the dorsal surface, the anteriormost occurring on the head and the posteriormost on the abdomen, the others belonging to the thoracic segments; 7 (or so) along the body margin mostly ventrally, the anteriormost occurring near the basal antennal segment and the posteriormost near the apex of the abdomen. Spiracles each with a 5-locular disc pore laterally. Antennae 3-segmented; basal segment broader than long, with 1 small seta; second segment very short, with 1 small seta; third segment about twice as long as broad, round apically, with 2 very long setae subapically and 9 (or so) setae variable in length but mostly fleshy. Legs robust; tarsi longer than the tibiae, in the hind legs about 1.5 times as long as the latter; tarsal digitules nearly as long as or (especially on the hind legs) a little shorter than the segment; claws gently curved, with a denticle subapically on the plantar surface; ungual digitules surpassing the claws. Anus indiscernible.

Adult female (Figs 3, 13, 14). Body round in outline, probably depressed subglobular when living; derm remaining membranous, with no trace of segmentation. There is a large, heavily sclerotized tubercle or "hump" in front of the anus; it is round in outline, more than 100 μ m in diameter, protuberant, but nearly flat over a broad dorsal surface, and entirely covered with a round, thin, but well-sclerotized operculum, which is fixed to the hump on the anterior margin (but liable to fall off during preparation) and densely areolate on the lower surface except marginally. The hump is surrounded by a sclerotized patch of derm, and these are surrounded by folds of derm; many folds running nearly transversely on the sides of the posterior half of the hump. There are 2 pairs of robust strong scleroses in front of the hump; when fully developed, these scleroses are elongate and directed towards the hump. The main features in the full-grown living insect may be positioned as shown in Fig. 3A, the hump being situated about the centre of the upper side. In the slide-mounted depressed specimens, the anus comes beneath the posterior end of the hump and is often rolled under the folded derm; it is a small opening surrounded by a sclerotized ring, and not always easily discernible owing to the hump and folded derm. Vulva also situated on the upper side, posterior to and at some distance from the hump, lying longitudinally on the midline of the body; it is accompanied with a pair of large, membranous, discoid structures anterolaterally. On the lower side, the mouth-parts are situated about the centre, with the anterior spiracles laterally and the posterior spiracles far lateroposteriorly; each spiracle is accompanied with a patch of minute granulations. No setiferous antennae present, but a pair of small sclerotized patches of derm, situated far anterolaterally to the mouth-parts, probably representing the rudiments of antennae. Legs lacking. No disc pores on both upper and lower sides. Minute ducts scattered in a broad area laterally to each spiracle. Long, apically swollen setae scattered on the operculum of the hump and the sclerotized patch of derm around the hump; a pair of similar setae present in front of the hump-associated scleroses and another pair laterally to the scleroses on each side of the body, both at some distance from the scleroses. Short setae scattered around the lateral to posterior margin of the hump and in a single or partly double longitudinal row between the hump and vulva, succeeded by some slender setae occurring on both sides of the vulva, all these setae forming a continuous series shaped like a Y. Short setae occurring also on other parts of the body, sparsely scattered mostly on the posterior half of the lower side. Minute angular processes strewn laterally to the hump; similar but a little larger processes strewn in ill-defined groups anterolaterally to the hump-associated scleroses at some distance from the latter. Small to minute granulations densely strewn on the lower side and also on the upper side posterior to the hump (that is, on the derm originally belonging to the ventrum of the body).

First-instar male (Fig. 4). Similar to the first-instar female, differing mainly in having smaller and less sclerotized dermal swellings. Some setae on the head and thorax not clavate but pointed. On the ventral surface, transverse rows of spicules occurring medially on the mesothorax through the succeeding segments to near the apex of the abdomen; ventral setae of the abdomen not crowded as in the first-instar female. Anus indiscernible as in the first-instar female.

Second-instar male (Figs 5, 15–19). Body elongate elliptical, round on both ends, with the lateral margins nearly parallel; segmentation rather distinct dorsally on the thorax and abdomen and ventrally on the abdomen. Clusters of 5-locular disc pores occurring in the submarginal region of the dorsal surface, one on each side of the head,

prothorax, and second to seventh abdominal segments; numbers of disc pores in each cluster: 12–23 on the head, 15–31 on the prothorax, 8–16 on the second abdominal segment, 7–15 on the third, 7–13 on the fourth, 7–12 on the fifth and sixth each, and 5–10 on the seventh (n=30; mode=8 on each of the second to seventh abdominal segments); total on both sides: about 160–210 (n=15); each of these disc pores is deeply concave, with the 5 loculi on the walls just within the periphery. Quinquelocular disc pores of the usual type present on the ventral surface: a few on the head and the meso- and metathorax submedially; and forming a submedian and a submarginal longitudinal series through the abdomen, mostly single on each segment. Tubular ducts occurring on both dorsal and ventral surfaces, scattered on the head and thorax but, on the abdomen, forming a median, an intermediate and a submarginal longitudinal series on the dorsal surface, and a submedian, a submarginal and a marginal series on the ventral surface, mostly single on each segment. Anterior spiracles each with a 5-locular disc pore. Long setae occurring on the head; thick clavate setae submedially and marginally on the dorsal surface of posterior abdominal segments; long submedian and marginal setae on the ventral surface of the abdomen; a pair of long thick setae at the apex of the abdomen. Transverse rows of spicules occurring on the ventral surface of the abdominal segments. Antennae 3-segmented; basal segment with an incomplete sclerotized ring, bearing 1 seta; second segment with a complete sclerotized slender ring, bearing 1 long seta; third segment about twice as long as wide, with 10 (or so) setae including 2 longer ones occurring on the apex. Legs moderate in thickness; tarsi a little longer than the tibiae, the tarsal digitules much shorter than the segment; claws gently curved, with a denticle near the apex on the plantar surface, the ungual digitules surpassing the claws. Anus small, situated at the apex of the abdomen.

Adult male (Fig. 6). Macropterous. Body robust, the head being about two thirds as broad as the thorax, and the abdomen except the genital segment about as long as the head and thorax combined; beset with "papillae" or nipple-like fleshy processes on the head and trunk; these papillae are slender, ending in a blunt apex, rather numerous on the head, restricted to some areas on the thorax, and mostly limited to the lateral area of the dorsal surface on the abdomen. A few slender fleshy processes are discernible on the second antennal segment and also on the subapical dorsal ridges of the mid and hind tibiae, and they may also be papillae. There are no disc pores; glandular pouches and accompanying long setae absent on the eighth abdominal segment. Head in dorsal view roughly square in outline; dorsal arm of the midcranial ridge absent; preocular ridge slender on the anterior margin of the dorsal eye; postocular ridge well represented on both surfaces; postoccipital ridge also well represented, laterally giving off 2 branches, one anteriorly and the other obliquely posteriorly. Eyes prominent; dorsal eyes about twice as large as the ventral eyes in the diameter of the cornea. Antennae about as long as the fore femur and tibia combined, 7-segmented; basal segment transversely rectangular in lateral view, the second globular, with hairy setae; the third constricted basally, gradually broadening apically, elongate, about twice as long as the second, with hairy setae and thickened setae (which are rather fleshy but pointed apically) towards the apex; fourth to seventh segments short, the fourth to sixth with hairy setae and thickened setae, the seventh with 6 fleshy setae and 6 long, stiff, and apically knobbed setae. Pronotal ridge well represented; no trace of post-tergite. Prescutum much longer than the scutum; scutellum transversely rectangular, well sclerotized. Postnotal apophysis developed. Mesosternum with the marginal ridge well represented, and with the furca developed and

sclerotized. Halteres absent. Legs rather slender; trochanter with the proximal portion much shorter than the distal, but not clearly demarcated from the latter; fore femora about as thick as the mid and hind femora; tibiae distinctly longer than the tarsi, about twice as long as the latter in the hind legs; tarsal digitules not recognizable (if they are present, they should be short and setose); claws slender, with a trace of a denticle subapically on the plantar surface, the ungual digitules slightly surpassing the claws. Abdomen with transverse rows of spicules well represented on the ventral surface and limited to posterior segments on the dorsal surface. Genital segment about as long as the preceding abdominal segments combined, swollen and conical basally, then produced into a slender style; a pair of minute but stiff setae occurring on the lateral margins of the style at some distance from the apex.

FEATURES AND A TAXONOMIC VIEW
[by TAKAGI]

In the following discussion by Takagi, the terms "feature" and "character" are used as in traditional taxonomy. They correspond respectively to "character" and "character-state" (or "characteristic") adopted in numerical phenetics and cladistics.

Features and their functions

Generally in gall-inhabiting coccoids, features tend to degenerate especially in the adult female. In *Danumococcus parashoreae*, this tendency has reached to such an extreme that the adult female has no setiferous antennae, no trace of legs, and no disc pores. In spite of this simplification, the adult female is provided with some remarkably developed structures—the heavily sclerotized eminent hump, the setiferous and areolate operculum covering the hump, and the strong scleroses in front of the hump, all these features having no similar structures in other coccoids. The female is also unusual in having the vulva lying longitudinally, in having a continuous series of dense setae from around the posterior half of the hump to around the vulva, and in having a pair of membranous discoid structures between the anus and vulva. These unique features and unusual characters must have developed in correspondence to the structure of the gall, but what is given below about their functions is no more than speculation.

The material had been preserved dry. Leaf pieces with galls were kept in a humid atmosphere sterilized by creosote for about one week before preparing coccoid specimens. In most of these softened galls containing a relaxed body of the adult female, the opening on the roof appeared to be plugged from the inside. On the body of the adult female, the only structure that can serve as a plug is the hump, which is large enough to stop the opening. The hard-shelled gall with the opening blocked by the strongly sclerotized hump may be effective against predators, parasites and other invaders, but the opening would need to be unplugged at least for copulation and escaping crawlers. The arrangement of the features around the hump may be explained on the following suppositions. The strong scleroses occurring in front of the hump should serve as attaching points of powerful muscles for moving the hump out of the opening of the gall and, thus, for applying the anus or the vulva to the opening. The supposed movement is made forwards and backwards, and in this manner of movement the longitudinal vulva on the midline of the body may more easily be applied to the opening than a transverse one. The dense setae occurring around the posterior half of the hump to around the vulva

must be involved in the sensory system controlling the movement. The membranous large discoid structures occurring between the anus and vulva should also have some function in connection with the movement, and a likely possibility is that they are suckers. In that case, they should be used for adhering the body to the ceiling of the gall, thus keeping the anus or, more probably, the vulva (which is closer to them than the anus) applied to the opening of the gall.

If the supposed manner of movement is real, the anus should be applied to the opening of the gall for excretion. The vulva may be exposed through the opening for releasing sex pheromone. Also at the time of copulation the vulva may be applied to the opening, but the adult male is provided with an elongated genital style, which is slender enough to be inserted deeply in the gall. It is, however, not easy to imagine how copulation is performed with the style inserted in the narrow gall. The limited interior space of the gall also offers the reason to suppose that the vulva is applied to the opening to send newborn crawlers immediately out of the gall. This assumption, requiring ovoviparity, is harmonious with the fact that the adult female does not possess any disc pores around the vulva (as well as elsewhere on the body) to powder eggs with wax. (SEM observations on some other coccoids have revealed that deposited eggs are coated with minute ring-shaped wax filaments secreted by disc pores.) In fact, no female crawlers were found within the gall. It should be mentioned, however, that some male nymphs of the first and second instars were obtained from within the gall in spite of the fact that male tests (cocoons) were found exclusively outside the gall on the lower surface of the leaf. The opening of the gall may be too small for male nymphs staying and growing in the gall to escape through it. Why do they remain within the gall? Is that merely due to their missing the chance of escape? What, then, will become of them? Does the gall eventually dehisce for their escape? No dehiscence, however, has been observed.

The quinquelocular disc pores occurring on the dorsal surface in the second-instar male are also noteworthy, because they form distinct clusters, thus differing from scattered ones usual in other coccoids, and also because each pore is deeply concave, thus dissimilar to the usual type of the quinquelocular disc pore. The male test or cocoon (Fig. 9) is a loose mass of wax (Fig. 10) secreted by the second-instar male. The dorsal portion of the test is composed of wax tubes and flattened wax filaments tangled together (Fig. 11); it is certain that the clustered disc pores produce these wax tubes, because the tubular ducts should secrete flattened filaments. In fact, the thickness of a wax tube approximately agrees with the diameter of each disc pore. The ventral portion of the test is composed of coiled wax filaments (Fig. 12) irregularly mingled with flattened filaments and tubes. The ventral quinquelocular disc pores, belonging to the usual type, should be responsible for these coiled filaments, while the tubes in the ventral portion are attributable to the dorsal origin. The clustered dorsal disc pores are the most numerous among the wax-secreting organs occurring on the second-instar male. Apparently, they have the dominant role in forming the cocoon, which is exposed on the lower surface of the leaf. It is worthy of attention that in other DGC's the males grow and metamorphose under the scales, or within the cavity, of the maternal gall, among the spinous external appendages of the gall, or in pit galls under the bark of the host plant, thus being completely concealed.

In *Mangalorea*, *Gallacoccus*, and *Echinogalla*, the first-instar nymphs are devoid of long caudal setae, the adult males are provided with a great number of papillae on the body and especially on the elongated trunk, and female crawlers and adult males emerge

synchronously from the same maternal galls. The combination of these conditions favours the supposition that female crawlers are phoretic on their winged brothers (Takagi, 2001), though the supposed phoresy is still to be confirmed by observing living material. In *Danumococcus parashoreae*, too, the first-instar nymphs are devoid of long caudal setae and the adult male is provided with papillae, though the papillae are limited to some parts of the body, which is not particularly elongated. In this species, too, female crawlers and adult males have been obtained from the same material, though the male normally completes its growth outside the maternal gall. The evidence for intersexual phoresy is circumstantial in all these DGC's and not fully compelling especially in *D. parashoreae*, but is not yet to be ignored altogether.

It should be mentioned here that the anus is not discernible in the first-instar female and male. In the adult females and nymphs of *Conchaspis* (Conchaspidae), too, the anus is not recognizable on slide-mounted specimens. In a SEM observation, however, it was clearly seen at the apex of the abdomen of an adult female in a view from behind the body (Takagi, 1992: Fig. 51). In the second-instar male of *D. parashoreae*, the anus is small but undoubtedly present at the apex of the abdomen.

A taxonomic view

The adult female of *Danumococcus parashoreae* is extremely degenerate in some ordinary features, and yet displays unusually modified characters and enormously developed peculiar features. It seems that, so far as this stage is concerned, there is no coccoid with which *D. parashoreae* can be adequately compared. Apparently, this is due to the adaptation of the adult female to the gall structure. The problem here is how to interpret this adaptation in taxonomic context.

It is impossible to deduce a fairly generalized ancestral form of *Danumococcus parashoreae* from the highly specialized adult female. The second-instar female is unknown, but it may also be modified in accordance with gall-inhabitation. The male normally lives outside the gall, and it is reasonable to expect that it is much less modified than the female. In fact, the second-instar male is more or less similar to those of other DGC's. It is, however, noteworthy in having clustered, deeply concave quinquelocular disc pores (Figs 15, 16) on the dorsal surface, because, while such concave quinquelocular disc pores are probably unusual in Coccoidea, similar disc pores and their clusters occur in the adult females and second-instar nymphs of *Dactylopius* (Fig. 20). As discussed in the preceding section, the clustered disc pores in *D. parashoreae* secrete wax tubes. In the present study, a SEM observation was made on a mass of wax deposited on the bottom of an alcohol vial containing material of *Dactylopius opuntiae* (collected at New Delhi, India, in 1978), but it was not successful in finding wax tubes in the mass. The clustered disc pores in the *Dactylopius* species differ from those in *Danumococcus* in containing "one or more tubular ducts which open inside the cluster" and "the pore, or outer part of the duct, is circular with a high thick ring toward the outside" (Perez Guerra and Kosztarab, 1992). According to Green (1926), "Female of third stage" in *Beesonia dipterocarpi* is characterized by having on the dorsum "two longitudinal series of twelve dense clusters of multilocular pores with, near the centre of each cluster, a single larger circular simple pore, the rim of which projects slightly above the surrounding surface" (the stage was corrected to "The next (3rd) stage in the male series" by Green, 1928; it is probably the second-instar male). The illustration accompanying the description of *B. dipterocarpi*, however, shows a loose group, instead

of a dense cluster, of quinquelocular disc pores, of which the detailed structure is unknown. (Hodgson examined the supposed second-instar male of a *Beesonia* species taken from Green's series. In a good specimen labelled "*Beesonia tuberculata*" [a manuscript name of *B. dipterocarpi* according to Hodgson] some of the dorsal disc-pore groups are quite densely packed, and many of these have a large tubular duct in their centre.) In the present state of our knowledge, it is not certain whether the clustered disc pores in *Danumococcus* (and the grouped ones in *B. dipterocarpi*) are homologous with those in *Dactylopius*, and, thus, whether their occurrence has any phylogenetic significance. (See also under "Taxonomic position based on the morphology of the adult male" by Hodgson.)

The significance of the occurrence of papillae on the adult male is also not clear but, whatever the function, the possibility that this unusual feature can be acquired by utterly unrelated forms may reasonably be doubted. In the antennae of this stage, *Danumococcus parashoreae* appears not much different from *Beesonia dipterocarpi* (described and illustrated by Green, 1926), the oak-associated *Beesonia napiformis* (described and illustrated by Hu et al., 1995), and *Mangalorea hopeae*, the third to seventh segments seemingly corresponding to the long third segment in the latter three species (and, thus, representing a primitive state as compared with the supposedly fused segments). In the genital segment elongated into a long, slender style or penis sheath, *D. parashoreae* is similar to the mentioned species of *Beesonia*. In this feature it is quite different from *Gallacoccus*, in which the penis sheath is short and curved below, but *Echinogalla* and *Mangalorea* come between them in the elongation of the penis sheath. Among all the known adult males of these genera, *D. parashoreae* is remarkably different in lacking glandular pouches and accompanying long setae on the eighth abdominal segment. However, losing something may be much easier than acquiring something new. The sclerites occurring on the head and thorax are well represented in *D. parashoreae*. In these features, *Echinogalla pustulata* appears much different from *Gallacoccus* and other DGC's, with some parts remarkably reduced or even obsolete, and yet it may have some phylogenetic affinity with *Gallacoccus* so far as based on their second-instar males (Takagi, 2001).

The first-instar nymphs of all the known DGC's and the oak-associated species of *Beesonia* are surprisingly similar in the antennae, which are three-segmented, with the basal segment broad and robust, the second very short, and the third elongate, robust, and domed apically, bearing some fleshy setae and a few slender ones. It seems that the antennae in the second-instar nymphs and the adult females are basically of this type, though they may be degenerative and modified especially in the adult females and are nearly obsolete in the adult female of *Danumococcus parashoreae*. It is not easy to decide whether the similarity in the antennae is due to convergence or has any phylogenetic significance. However, the first-instar nymphs of other gall-inducing coccoids are generally provided with longer antennae with more numerous segments. It should not be overlooked that the first-instar female and male of *D. parashoreae* are similar to those of *Echinogalla pustulata* in other features, too, except that the anus in the latter is clearly seen, being surrounded by a thick rim bearing robust setae in the female, in contrast to the indiscernible anus in the former.

The adult females of *Mangalorea*, *Gallacoccus*, and *Echinogalla* are commonly characterized in having enormously developed "aliform scleroses" on the mouth-parts. It seems that the adult female of *Danumococcus parashoreae* is provided with a

corresponding structure, which is, however, not remarkably developed (Fig. 3) (and, therefore, not mentioned in the diagnostic description above).

The particular features discussed above, when taken separately, lead us to conflicting views. Emphasis laid on the peculiar features in the adult female of *Danumococcus parashoreae* may make the erection of a new isolated family valid. Yet some features in the first-instar female and the first- and second-instar and adult males in *D. parashoreae* are similar to those in other DGC's and the oak-associated species of *Beesonia* in various degrees. These stages as a whole support the view that all these species belong to a phylogenetically significant group. On the other hand, if the occurrence of the clustered, deeply concave quinquelocular disc pores has any phylogenetic significance, the possibility that *D. parashoreae* (and also *Beesonia dipterocarpi*) has some relation to *Dactylopius* may not be rejected. This in turn may promote the concept of a broader natural group comprising all DGC's and the oak-associated species of *Beesonia*, *Dactylopius*, *Eriococcus* and related genera, and other genera now in separate families. This concept is not entirely new, approaching Hoy's (1963) interpretation of the family Eriococcidae.

On the basis of surveys of gall-bearing herbarium specimens collected in Asia, Africa, and Madagascar, Jenkins and Mabberley (1994) adopted the view that the association of gall-inducing coccoids with dipterocarps has its origin in the early Cretaceous period, approximately 140 million years ago, on Gondwanic malvalean/dipterocarpaceous ancestors, and that drifting India carried gall-inhabiting coccoids on dipterocarps from Africa into Asia. It follows that, during more than 100 million years, dipterocarps and DGC's have evolved under the influence of dramatic geological events, both global and regional, and especially of those that have formed the complicated topography of tropical Asia. During the Late Oligocene and Early Miocene, dipterocarps were already extensively represented in the Sunda region (Morley, 2000). A gall-inhabitant (provided it is not an invader) does induce a gall, which, however, should be a phenotypic manifestation of the host plant's genomic potential (as indicated by the galls induced by some DGC's: see Anthony, 1977, and Jenkins and Mabberley, 1994). No doubt an essential aspect in the evolution of gall-inhabitants is adaptation to galls developed by their host plants, which also evolve. New characters and novel features may appear on gall-inhabitants in combination with conserved characters, degenerate features, convergence, parallelism, atavism, and so on. We may expect that the ancient origin and the geological change have contributed to bring forth a phylogenetically significant and yet morphologically and behaviourally diversified group of gall-inhabiting coccoids on dipterocarps. Thus, all DGC's, together with the oak-associated *Beesonia* species, which represent a host expansion, may constitute a higher taxon—the family Beesoniidae. This view is tentative, because the possibility that there is a broader natural group comprising all these forms, *Dactylopius*, and many others now in different families cannot be excluded as discussed above. The known beesoniids, which are few and yet far from uniform, suggest the validity of dividing the family into some subgroups. Especially, *Danumococcus parashoreae* is peculiar in the morphological pattern of the adult female apparently in a close correspondence to the structure of the gall normally inhabited by the female alone. However, the known forms undoubtedly represent too small a fraction of the family to establish formal subgroups.

In the following section, Hodgson concludes that the stictococcids are closely related to the beesoniids despite the adult females being structurally very different. The

adult female stictococcids are unique in having the "anal apparatus" situated centrally on the dorsum. The migration of the anus into an unusually anterior position is not restricted to the stictococcids. In the adult female of a diaspidid, *Roureaspis dungunensis*, the anus is situated not on the pygidium but on the preceding segment, which is interpreted to be the fourth abdominal segment (Takagi et al., 1997).

TAXONOMIC POSITION

BASED ON THE MORPHOLOGY OF THE ADULT MALE

[by HODGSON]

Introduction

As indicated in the discussion above, there are perhaps no characters on the adult female which can be used to indicate the relationships of *Danumococcus parashoreae*, and rather too little is known about the immature stages of most of the possible relatives of this species to be much help either, although the clustered quinquelocular pores on the second-instar male of *D. parashoreae* (and *Beesonia dipterocarpi*) do suggest a possible relationship with the Dactylopiidae. On the other hand, the adult male of *D. parashoreae* is a reasonably typical macropterous adult male coccoid with many characters which might be used for looking at possible relationships. Males of most neococcoid families have been studied by Hodgson, and his study of the adult males of about 16 mainly neococcoid families produced a preliminary cladogram indicating their possible relationships (Hodgson, 2001). The opportunity was taken, therefore, to add *D. parashoreae* to that data base. From the above discussion by Takagi, it is clear that the main purpose of this analysis was to see (i) whether it would indicate into which family *D. parashoreae* should be placed, (ii) what other families might be considered to be closely related and (iii) what, if anything, this analysis would tell us about the evolution of this odd species.

Materials and methods

The analysis was similar to that done by Hodgson (2001), with four species of Ortheziidae as the outgroup. The ingroup included a further 102 taxa belonging to 16 families. The analysis used 145 characters and was run using Hennig86, using *mhennig* followed by the *bb* option (Farris, 1988). All characters were equally weighted and unordered. A strict consensus tree was generated using the *nelson* command. For further information, see Hodgson (2001).

Results

Because this is part of a much larger on-going research programme looking at the relationships of the higher taxa within the Coccoidea based on the morphology of the macropterous male, only that part of the tree which relates to the present problem will be discussed here as most of the rest of the cladogram is not relevant to the present study. In addition, because the lists of (a) 145 characters and character-states, (b) the large data matrix and (c) the list of species used in the analysis would require much space, these will be included in a later publication. Should a reader need this information, it will willingly be made available by the author.

From the base of the complete consensus tree arise various clades (not shown) which include the Phenacoleachiidae, Putoidae, Pseudococcidae and some of the

Eriococcidae. At this point there is a trichotomy (Fig. 21): a node from which arise the gall-inducing eriococcid genera *Callococcus*, *Lachnodius* and *Calycicoccus* (Clade A); a node from which arises a clade (Clade B) into which *Danumococcus* falls, and a third node from which arise all the rest of the neococcoids (Clade C). The following discussion relates to the node numbers on Clade B in Fig. 21.

At node 1, the Dactylopiidae are sister to the remaining taxa. Nodes 2–4 inclusive relate to four gall-inducing Australian "eriococcid" genera, one of which is sister to the taxa arising from node 5. At node 5, there is a dichotomy in which the Beesoniidae (plus *D. parashoreae*) (node 6) are sister to the Stictococcidae (node 7).

Discussion

The dichotomy at node 1 in Fig. 21 has the Dactylopiidae sister to the eriococcid/beesoniid/stictococcid clade. The dactylopiid clade is diagnosed by 14 character-state changes. The dactylopiids do not induce galls but still fall within Clade B which otherwise contains many species which are gall inducers. The family status of the Dactylopiidae has been questioned recently by Gullan and Cook (1999) who believe that this taxon falls within the eriococcids based on nucleotide sequence data from the small unit rDNA gene (18S). Their more recent work (Cook et al., 2002; Cook and Gullan, 2004) supports this view. From all of these studies, it is clear that the Dactylopiidae are at least very close to the Eriococcidae. (For further discussion, see below.)

From nodes 2, 3 and 4 arise four species of Australian gall-inducing coccoids currently placed in the Eriococcidae (Fig. 21): *Apiomorpha spinifer*, *Cystococcus echiniformis*, *Opisthoscelis verrucula* and *O. subrotunda*. This is not a monophyletic group but the basal node for these four species plus the beesoniid/stictococcid clade is diagnosed by nine character-state changes.

The clade containing the Beesoniidae plus the Stictococcidae (node 5) is diagnosed by 25 character-state changes, strongly suggesting that these two families might be closely related, despite the adult females being structurally so different. This relationship was noted previously by Hodgson (2001) with adult males, and Cook et al. (2002) and Cook and Gullan (2004) based on small unit DNA studies. The stictococcid clade (node 7) is diagnosed by 11 character-state changes and the beesoniid clade by three character-state changes. Each successive node within the Beesoniidae is diagnosed by 6–8 character-state changes.

The above analysis considers only adult male characters. Adult female stictococcids are unique amongst the Coccoidea in having the "anal apparatus" situated centrally on the dorsum. The reasons for the anus being in this position are unclear but, as both the beesoniids and the Australian eriococcids (nodes 2–4) are all gall inducers, this analysis suggests that the stictococcids might have arisen from gall-inducing ancestors. If so, the need to eliminate their waste through the gall aperture might have caused the anus to migrate to a mid-point on the dorsum. In addition, the adult males have very long penial sheaths (genital style of Takagi above). Long penial sheaths appear to be characteristic of many gall-inducing coccoids, again suggesting that the females could once have lived inside plants, requiring the males to have long penial sheaths in order to copulate.

With regard to node 6, this analysis suggests that *Danumococcus parashoreae* should be included in the Beesoniidae. Interestingly, the anus of *D. parashoreae* lies beneath the posterior margin of the sclerotized tubercle—and so the position of the anus is similar to that on female Stictococcidae, even if the structure of the anus is probably

very different.

Cook and Gullan (2004) consider the evolution of gall induction in a range of scale insect families and have *Beesonia napiformis*, *Gallacoccus heckrothi* (a beesoniid) plus *Stictococcus sjostedti* (plus some gall-inducing and non-gall-inducing eriococcids) in a clade sister to two clades of Eriococcidae. In one of these two clades, all the species are gall inducers (including *Lachnodius* sp., *Opisthoscelis mammularis* and *Cystococcus echiniformis*). Cook and Gullan also included three species of *Apiomorpha* in their study but these fall outside the *Lachnodius/Opisthoscelis* clade. The species shared by our present study and by Cook and Gullan's study therefore lie in more or less the same places in the two cladograms. However, on the basis that each of the gall inducers included in their study had a non-gall-inducing sister taxon in which the adult female morphology was apparently of the plesiomorphic eriococcid type, Cook and Gullan conclude that the gall-inducing habit probably arose several times among the taxa they included in their study. In the present analysis, all four of the eriococcid species in Clade B are gall inducers, suggesting that the beesoniid/stictococcid clade could have had a gall-inducing ancestor (see discussion below) although Cook and Gullan's cladogram does not support this suggestion.

In this analysis, *Danumococcus* is sister to the rest of the Beesoniidae. Takagi speculates above on whether the ancestors to present-day Beesoniidae were carried by a drifting India from a disintegrating Gondwana during the Cretaceous. Thus, if the ancestors to present-day Beesoniidae and Stictococcidae were gall inducers at the time that Gondwana was breaking up, perhaps with their anal apparatus mid-dorsally, then the lineage which gave rise to present-day Stictococcidae could have remained isolated in Africa, coming to live outside galls, developing a highly sclerotized cuticle in the adult female, presumably for protection, but also retaining a mid-dorsal anus and relying on ants for honeydew removal. The lineage on the drifting India would then appear to have remained as gall inducers and to have given rise to the present-day beesoniids, perhaps with the adult female *Danumococcus* retaining the anus on the mid-dorsum.

With regard to a possible gall-inducing ancestor to the Stictococcidae, Newstead (1910) described *Stictococcus formicarius* as living in a "marked depression or pit" within the hollow stems of its host, which also caused a "slightly raised and irregular prominence" on the outer surface of the twig.

Takagi points out above that the groups of quinquelocular pores on second-instar male *D. parashoreae* (and similar groups are present on *Beesonia dipterocarpi*) are not dissimilar to those on dactylopiids and speculates about a possible relationship between these two taxa. From the above analysis, it would seem unlikely that these pore clusters are homologous. However, Takagi also speculates on whether there might be a broader natural group comprising the beesoniids, dactylopiids and other families. The above analysis certainly suggests that, as suggested by Gullan and Cook (1999), the Dactylopiidae fall within the Eriococcidae, as also do the beesoniids and stictococcids, as they also appear to do in Cook and Gullan (2004).

Conclusions

Based on this cladistic study using only macropterous male characters:

1. *Danumococcus parashoreae* falls within the beesoniid clade and should be considered to belong to the Beesoniidae.
2. The closest relatives to the Beesoniidae are the Stictococcidae.

3. Both the Beesoniidae and Stictococcidae fall within a larger clade which also includes the Dactylopiidae and some gall-inducing eriococcids.
4. It is speculated that the Beesoniidae and the Stictococcidae arose from a common, gall-inducing ancestor, probably within the Eriococcidae, thus accounting for the unusual position of the anal apparatus on adult female Stictococcidae.

COCCOID GENERA AND SPECIES
MENTIONED IN THE TEXT AND FIG. 21

Apiomorpha Rübsaamen, 1894; *A. spinifer* Froggatt, 1930.

Beesonia Green, 1926; *B. dipterocarpi* Green, 1926; *B. napiformis* (Kuwana, 1914); *B. shoreae* Takagi, 1995.

Callococcus Ferris, 1918; *C. pulchellus* (Maskell, 1897).

Calycicoccus Brain, 1918; *C. merwei* Brain, 1918.

Conchaspis Cockerell, 1893.

Cystococcus Fuller, 1897; *C. echiniformis* Fuller, 1897.

Dactyliopius Costa, 1835; *D. confusus* (Cockerell, 1893); *D. opuntiae* (Cockerell, 1896).

Echinogalla Takagi, 2001; *E. pustulata* Takagi, 2001.

Gallacoccus Beardsley, 1971; *G. anthonyae* Beardsley, 1971; *G. heckrothi* Takagi, 2001; *G. secundus* Beardsley, 1971; *G. spinigalla* Takagi, 2001.

Lachnodius Maskell, 1896; *L. eucalypti* (Maskell, 1892).

Limacoccus Bondar, 1929.

Mangalorea Takagi, 1992; *M. hopeae* Takagi, 1992.

Opisthoscelis Schrader, 1863; *O. mammularis* Froggatt, 1894; *O. subrotunda* Schrader, 1863; *O. verrucula* Froggatt, 1894.

Parastictococcus Richard, 1971; *P. brachystegiae* (Hall, 1935); *P. gowdeyi* (Newstead, 1913); *P. hargreavesi* (Vayssiére, 1935).

Roureaspis Takagi, 1997; *R. dungunensis* Takagi, 1997.

Stictococcus Cockerell, 1903; *S. formicarius* Newstead, 1910; *S. intermedius* Newstead, 1917; *S. multispinosus* Newstead, 1908; *S. sjostedti* Cockerell, 1903; *S. vayssierei* Richard, 1971.

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Fig. 1. *Danumococcus parashoreae*: galls and male tests on the lower surface of a leaf (dry material). In this picture, five galls open on the lower surface of the leaf and the others on the upper surface. Scale in millimetres.

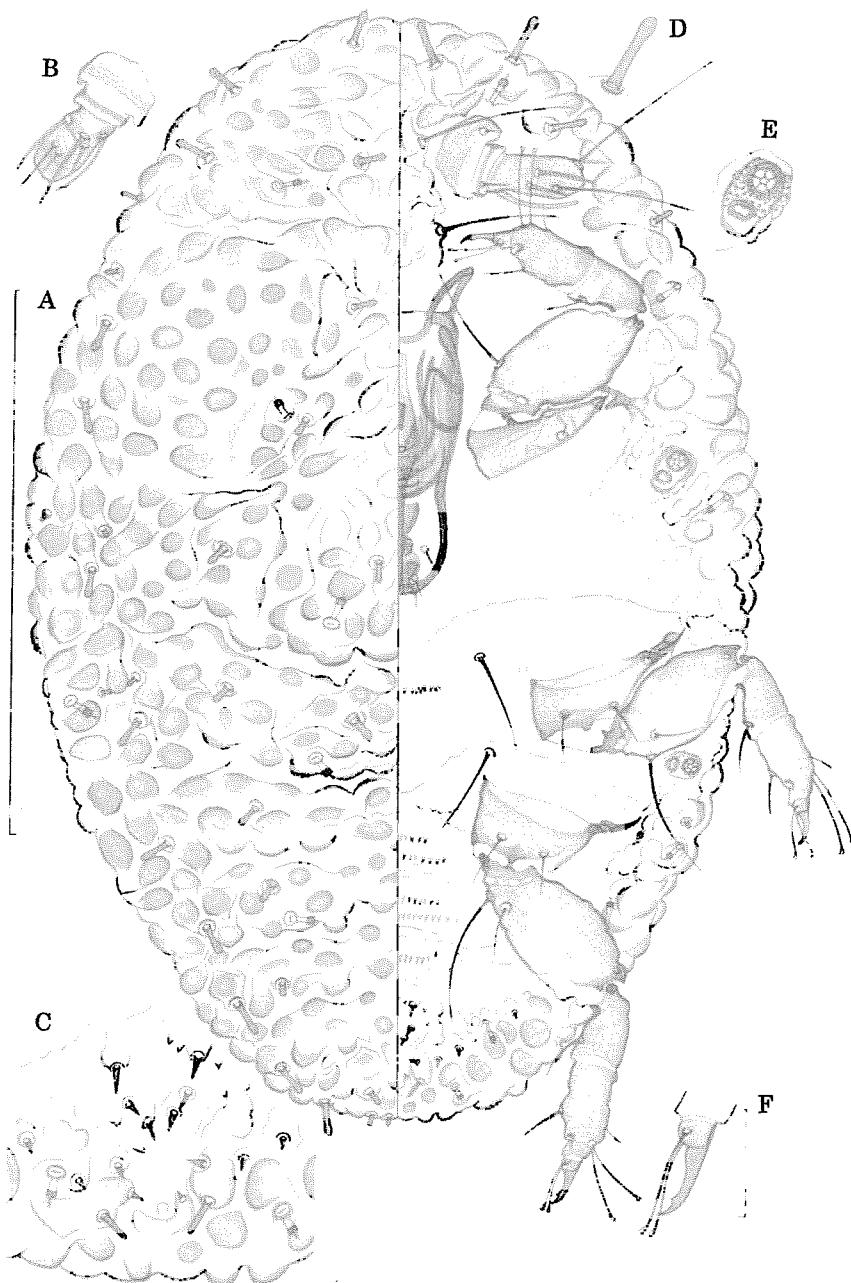


Fig. 2. *Damumococcus parashoreae*: first-instar female. B, antenna in dorsal view (in another specimen); C, apex of the abdomen in ventral view; D, marginal spine on the head; E, anterior spiracle; F, claw of the hind leg. Scale bars: A, 100 μ m (B magnified at the same rate as A); F, 10 μ m (C-E magnified at the same rate as F).

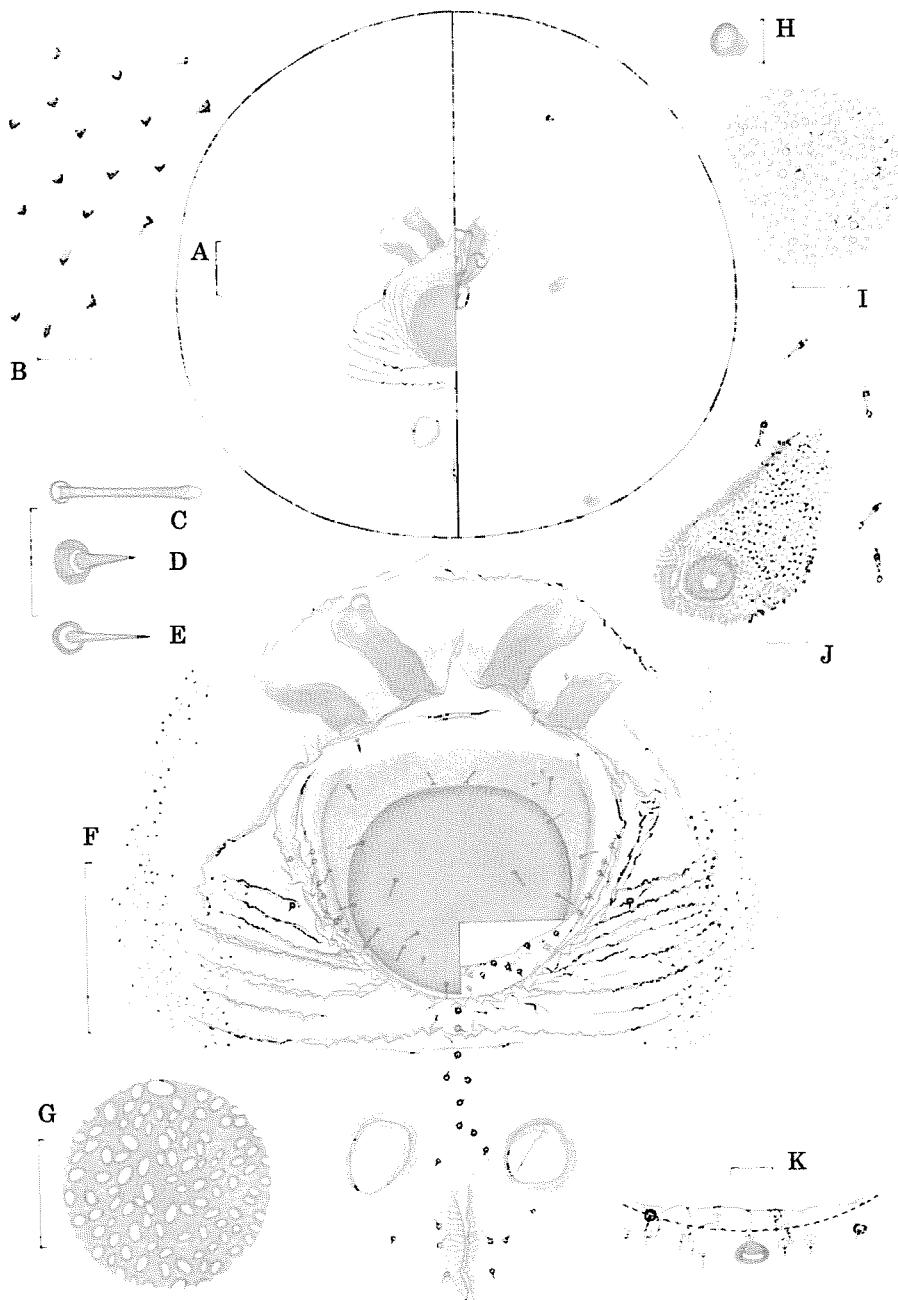


Fig. 3. *Danumococcus parashoreae*: adult female. B, minute angular processes laterally to the hump; C, type of setae occurring on the operculum of the hump and the sclerotized patch of derm around the hump; D, type of setae occurring around the lateral to posterior margin of the hump; E, type of setae occurring around the vulva; F, body part including the hump and vulva; G, areolations on the lower surface of the operculum covering the hump; H, antenna; I, granulations on the ventral surface; J, anterior spiracle; K, anus. Scale bars: A and F, 100µm; B-E and G-K, 10µm.

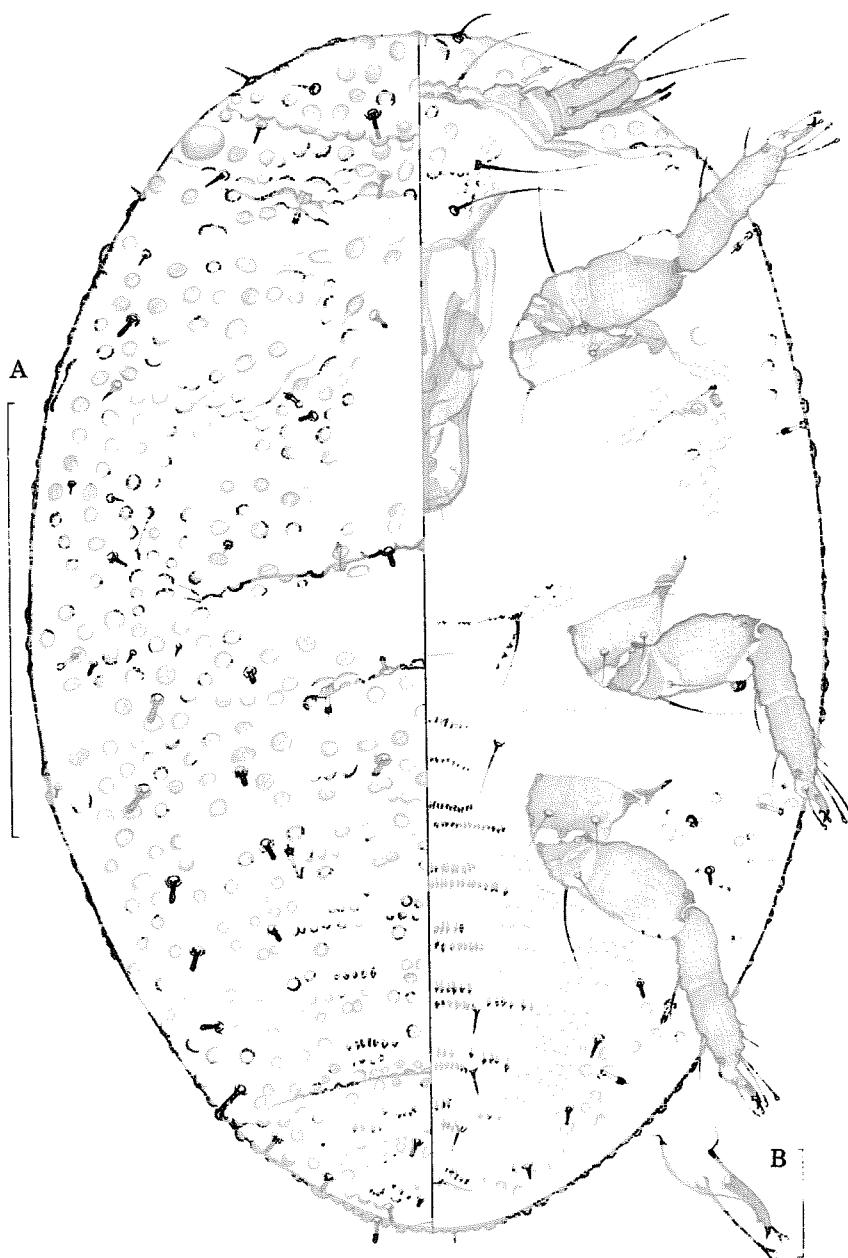


Fig. 4. *Danumococcus parashoreae*: first-instar male. B, claw of the hind leg. Scale bars: A, 100 μ m; B, 10 μ m.

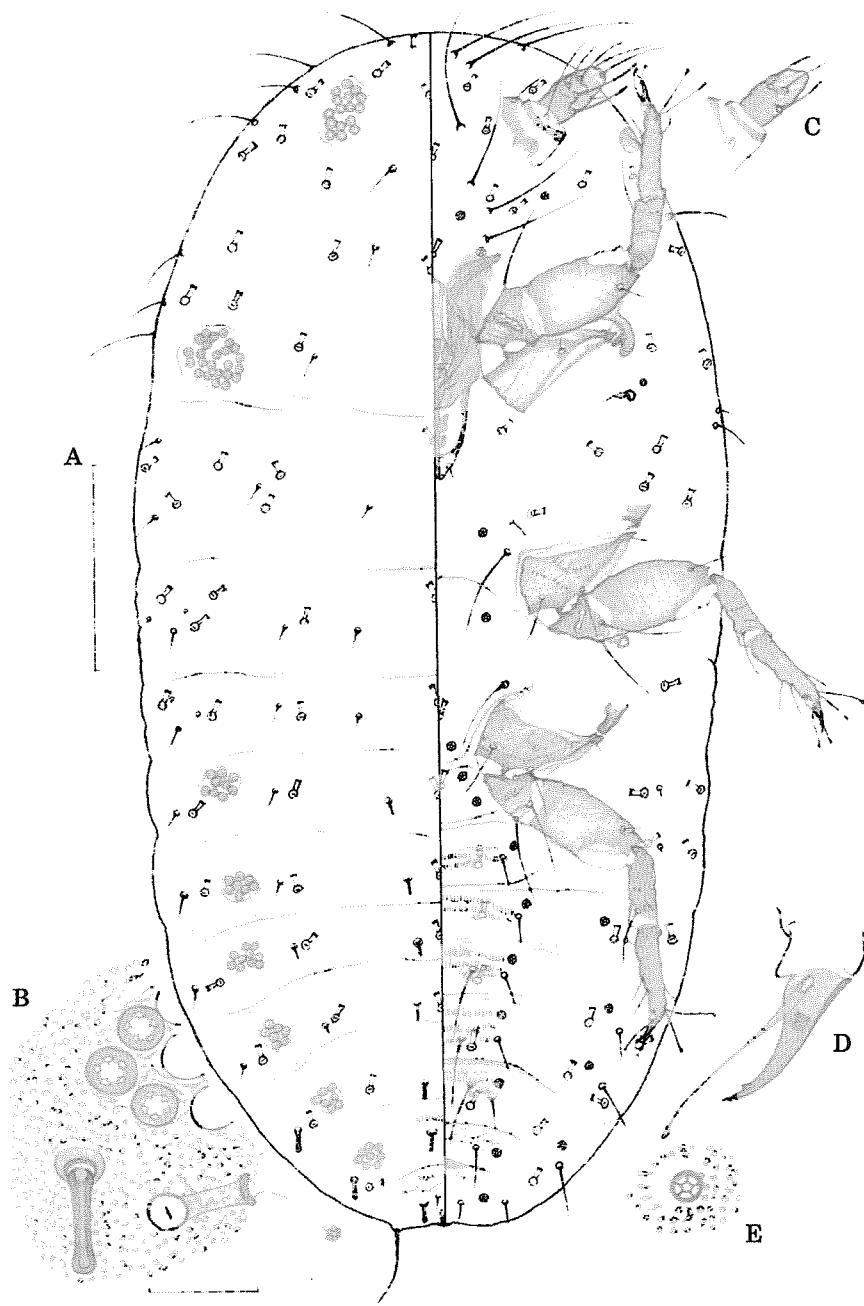


Fig. 5. *Danumococcus parashoreae*: second-instar male. B, cluster of disc pores (part), marginal duct, and marginal seta on the dorsum of the seventh abdominal segment; C, antenna in dorsal view; D, claw of the hind leg; E, ventral disc pore. Scale bars: A, 100 μ m; B, 10 μ m (C-E magnified at the same rate as B).

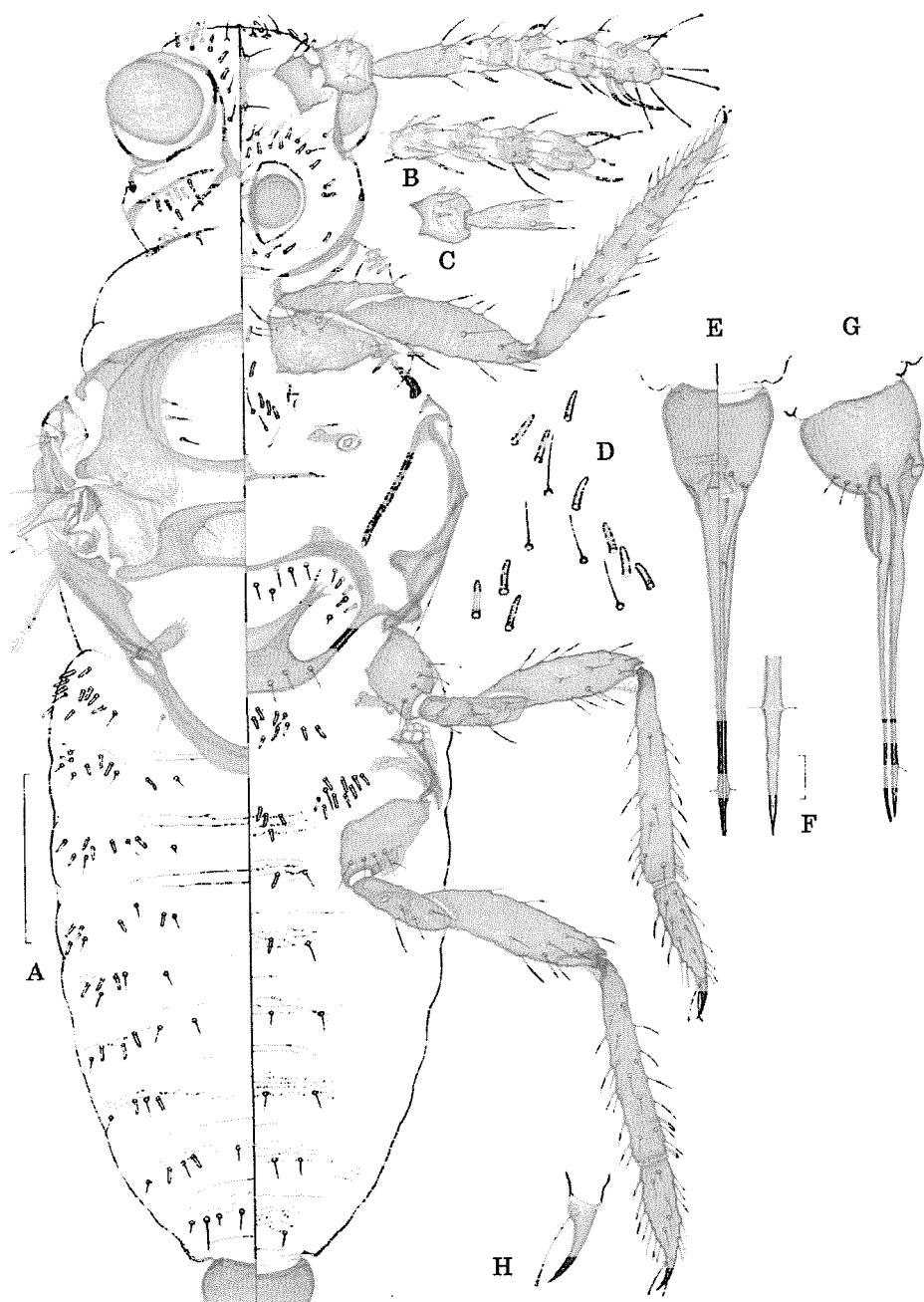


Fig. 6. *Danumococcus parashoreae*: adult male. A, body (figured by combining different parts of five specimens), with the genital segment shown in E and G; B and C, second to seventh antennal segments in dorsal view; D, papillae between the fore coxae; E and G, genital segment in dorsoventral and lateral views; F, part of the genital style to show the subapical setae; H, claw of the hind leg. Scale bars: A, 100 μ m (B, C, E, and G magnified at the same rate as A); F, 10 μ m (D and H magnified at the same rate as F).

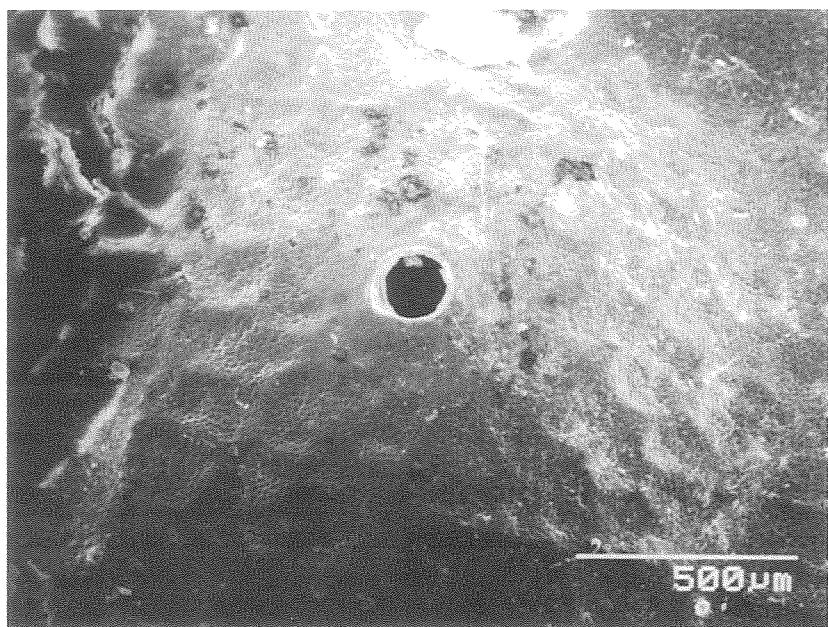


Fig. 7. *Danumococcus parashoreae*: gall in external view, roof.

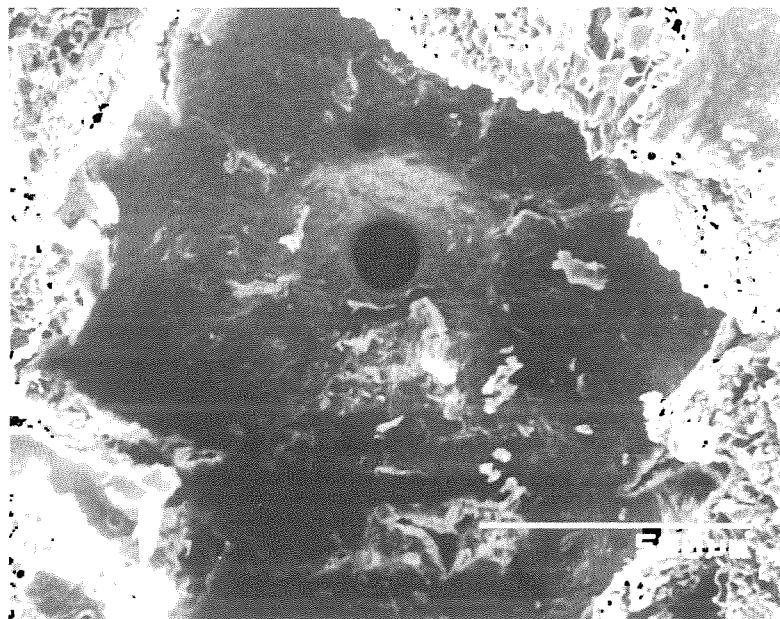


Fig. 8. *Danumococcus parashoreae*: gall in internal view, ceiling.

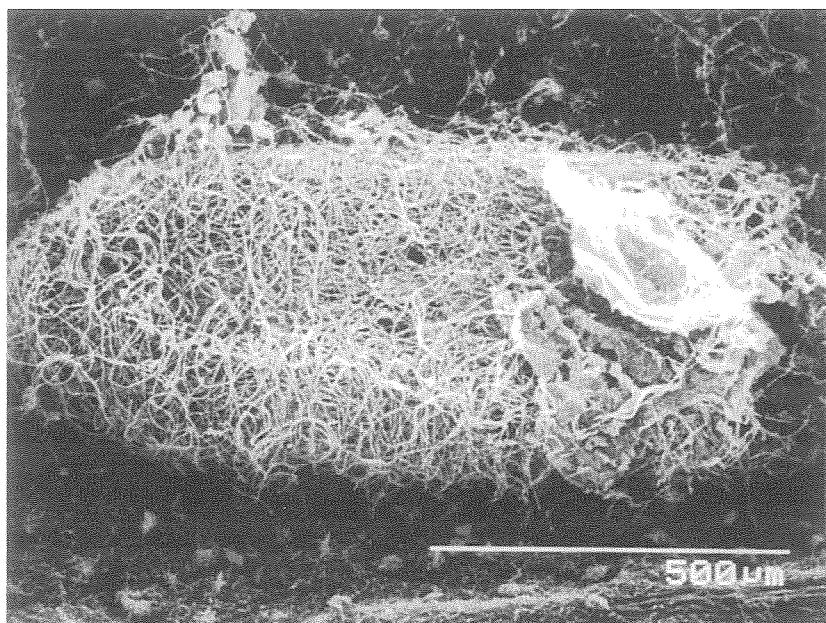


Fig. 9. *Danumococcus parashoreae*: male test in dorsal view.

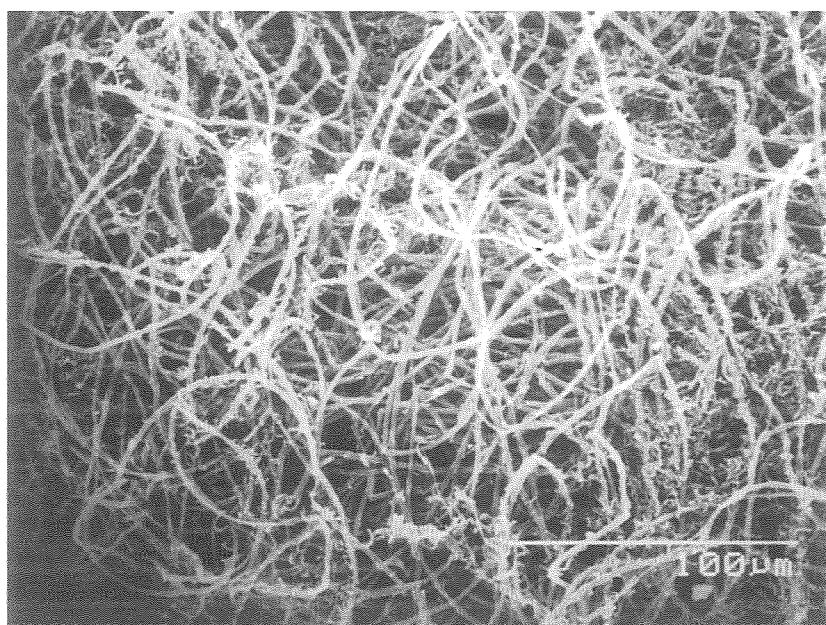


Fig. 10. Part of Fig. 9, showing wax filaments.

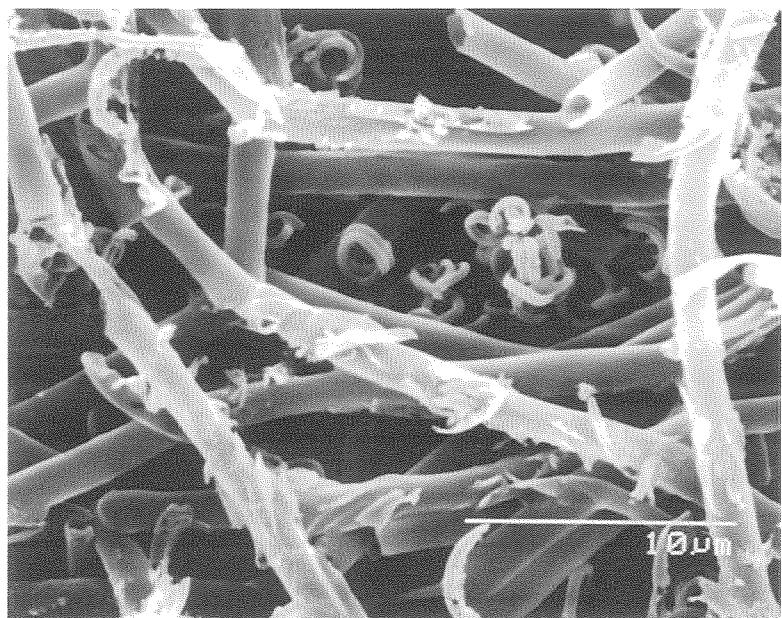


Fig. 11. *Danumococcus parashoreae*: male test, wax filaments in the dorsal portion.

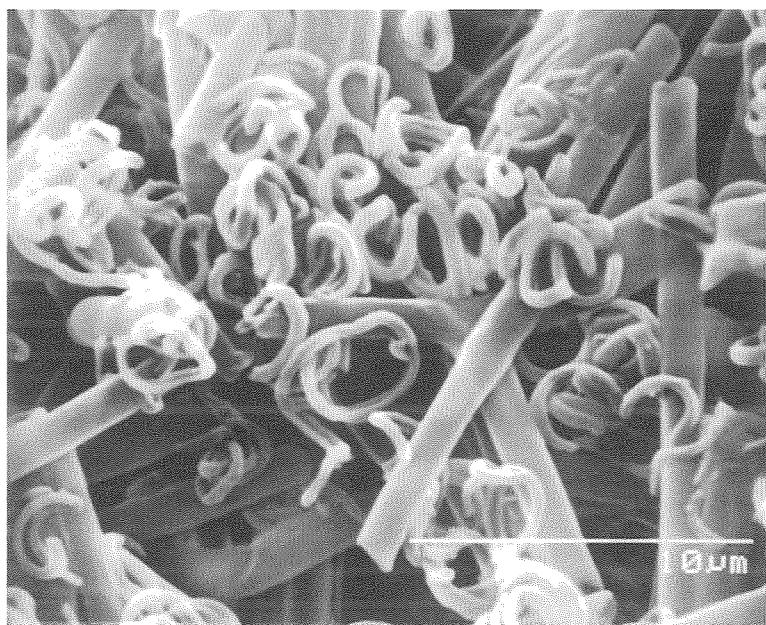


Fig. 12. *Danumococcus parashoreae*: male test, wax filaments in the ventral portion.

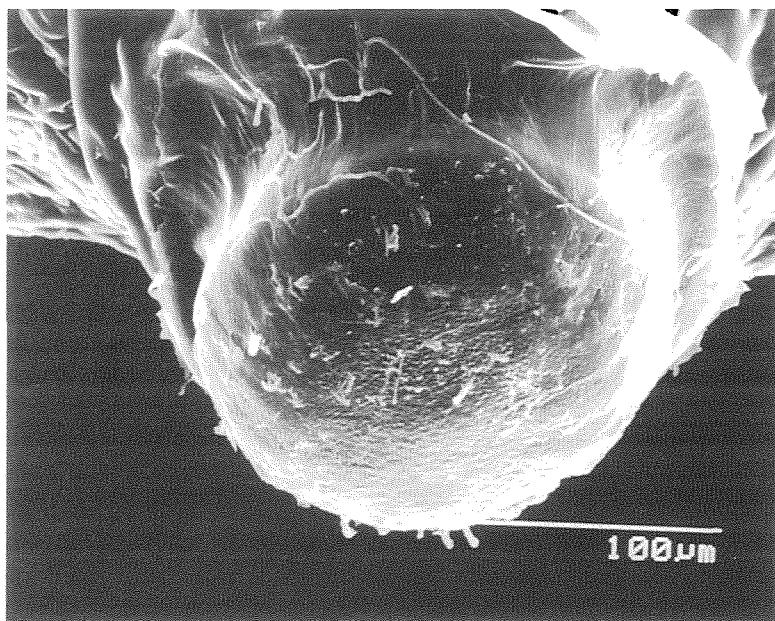


Fig. 13. *Danumococcus parashoreae*: adult female, hump seen from above.

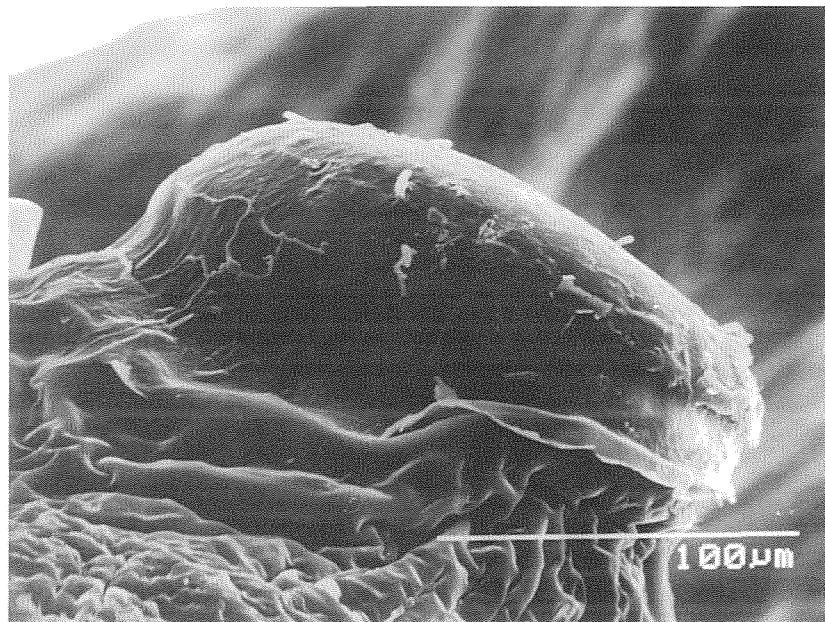


Fig. 14. Same as Fig. 13, in lateral view (left side of the photograph: anterior direction of the body).

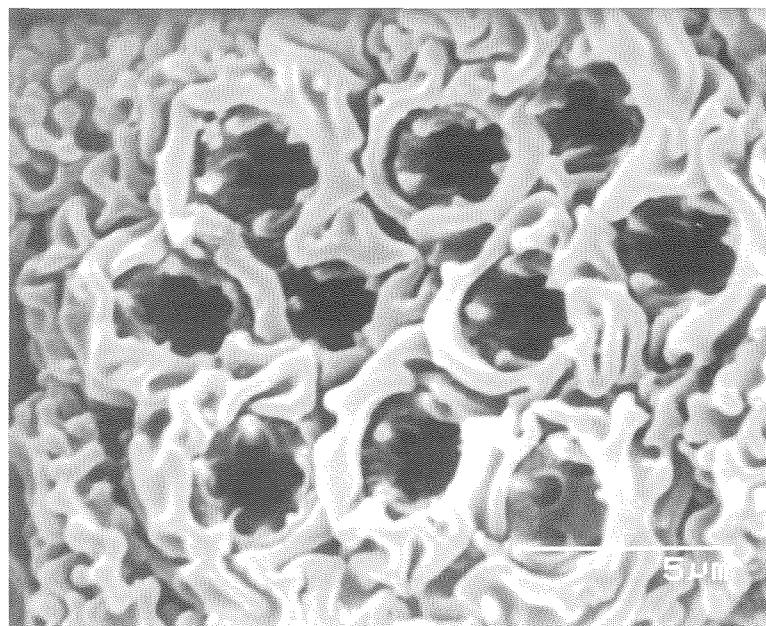


Fig. 15. *Danumococcus parashoreae*: second-instar male, cluster of dorsal disc pores.

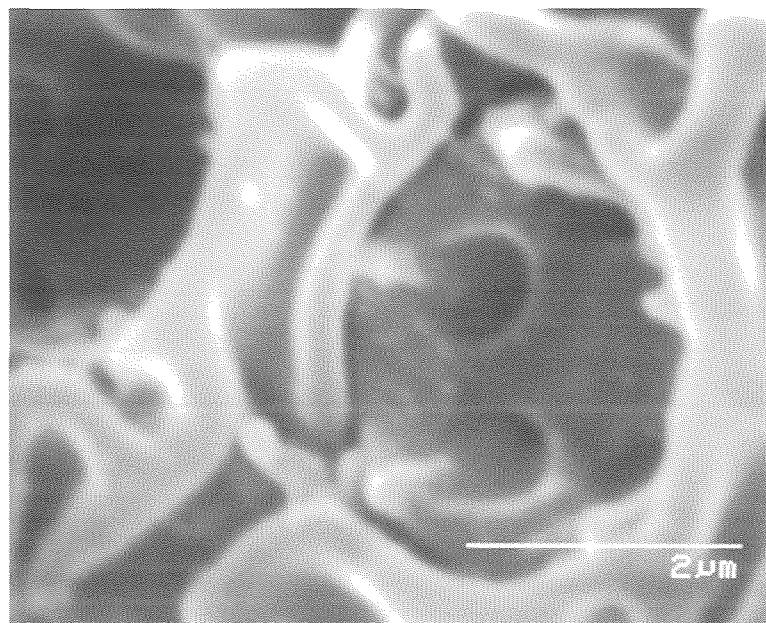


Fig. 16. Part of Fig. 15, showing one of the disc pores.

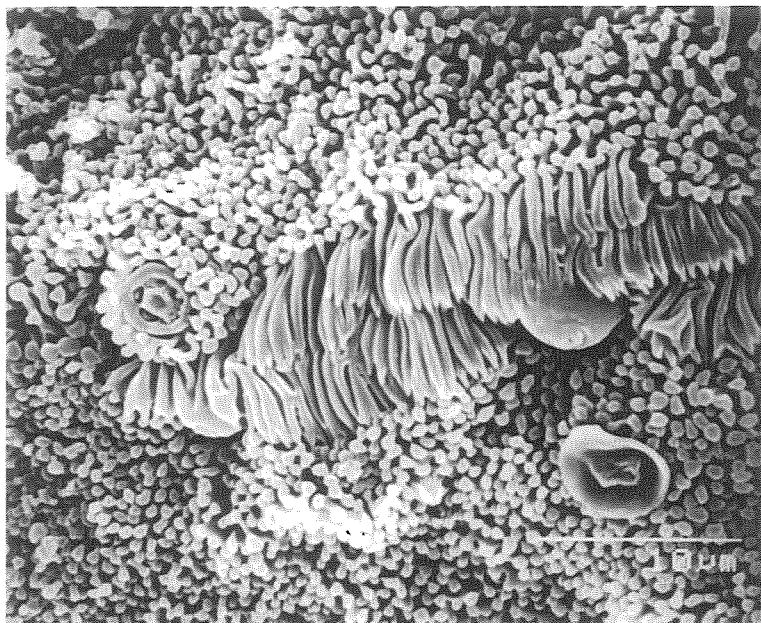


Fig. 17. *Danumococcus parashoreae*: second-instar male, part of the ventral surface of the abdomen.

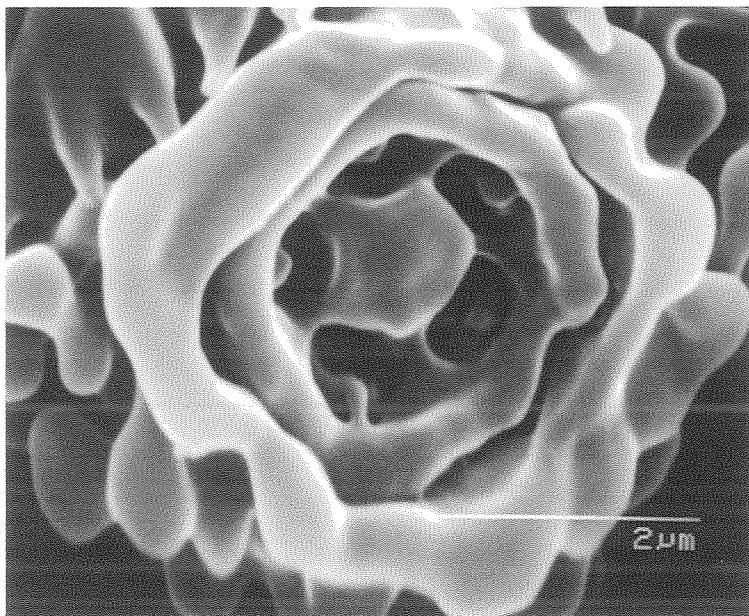


Fig. 18. *Danumococcus parashoreae*: second-instar male, ventral disc pore.

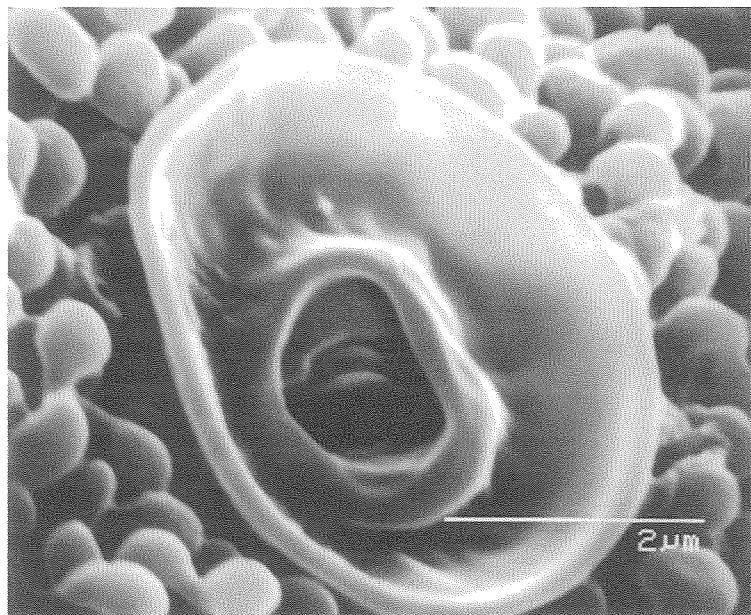


Fig. 19. *Danumococcus parashoreae*: second-instar male, opening of a duct.

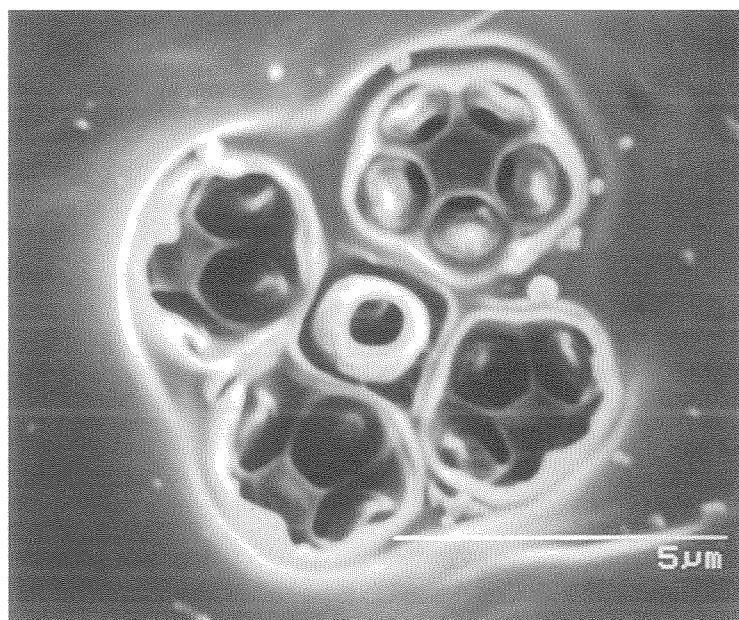


Fig. 20. *Dactylopius opuntiae*: adult female, cluster of disc pores. (The material was obtained at New Delhi, India, on a cactus, probably *Opuntia* sp., in 1978.)

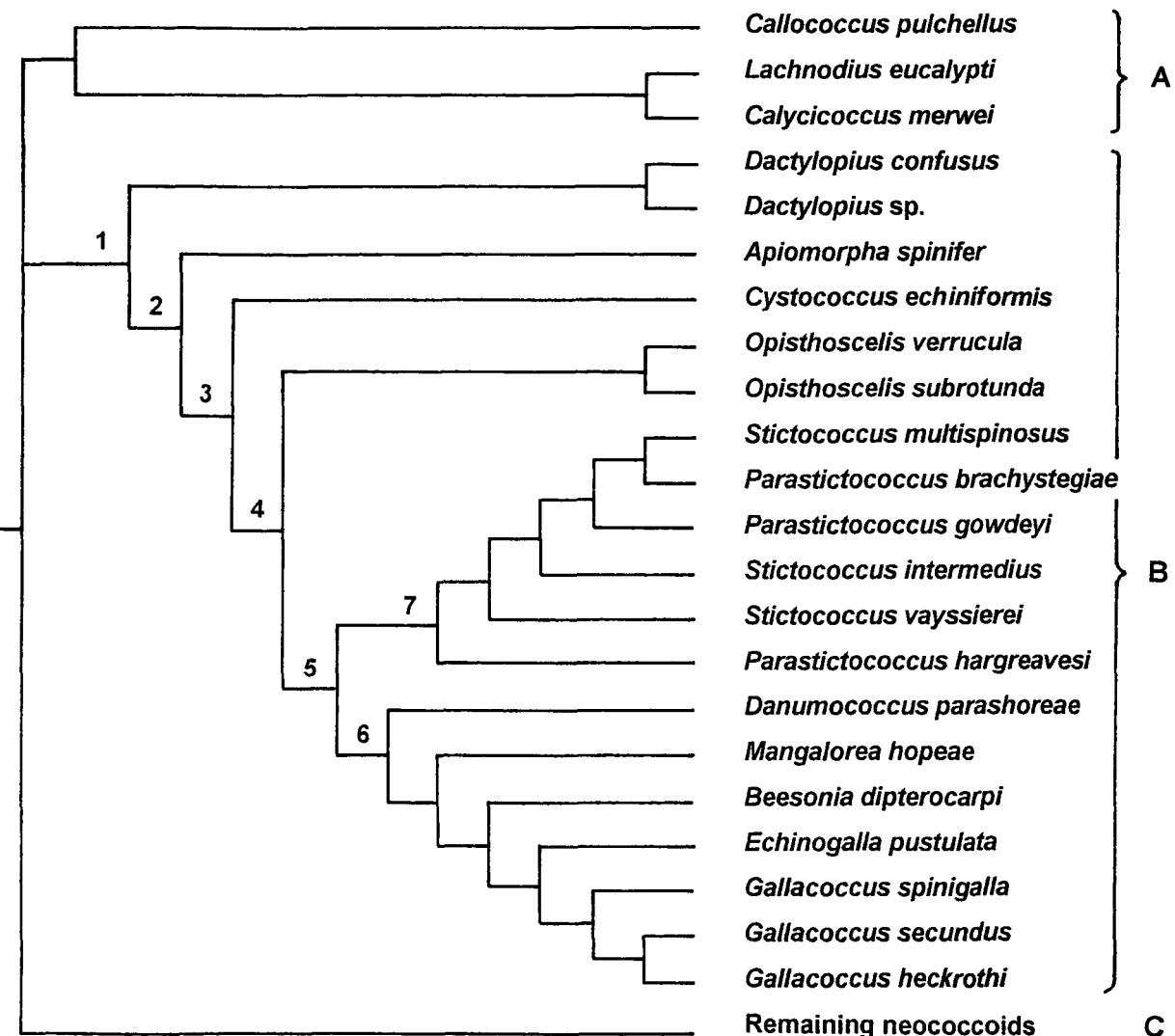


Fig. 21. Part of a strict consensus cladogram using Hennig86: *mhennig* followed by *bb* and *nelson*.

The complete analysis included 102 taxa and 145 characters; character-states unordered; statistics for complete cladogram: *L* 1768, *CI* 15, *RJ* 69. This part of the cladogram shows a trichotomy from which arise clades A (going to three Eriococcidae), B (the subject of this part) and C (the remaining neococcoids). The numbers at some nodes in Clade B are referred to in the text but at node 1 the Dactylopiidae are sister to the remaining taxa; from nodes 2, 3 and 4 arise four gall-inducing Eriococcidae and these are sister to the taxa in node 5, which has the Stictococcidae (node 7) sister to the Beesoniidae (node 6). *Danumococcus parashoreae* arises from node 6 and is sister to the remaining Beesoniidae.